

New fossil species of *Phlebotomus* and *Haematopota* in Baltic Amber (Diptera: Psychodidae, Tabanidae)

by

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SYNOPSIS

Descriptions are given of *Phlebotomus succini* sp. n. (Psychodidae) and *Haematopota pinicola* sp. n. (Tabanidae) fossilized in Baltic Amber. *P. succini* is compared with *P. tipuliformis* Meunier of the Baltic Amber fauna and with the species of *Phlebotomites* Hennig in Neocomian Lebanese Amber. A possible synonymy of *Phlebotomites* and *Phlebotomiella* Meunier is indicated. *P. succini* is not related to any of the fossil species, and cannot be allocated to any subgenus erected for living species. The formation and possible evolution of the wing pattern in *Haematopota* is discussed; the wing of *pinicola* resembles that of a modern African savanna species in certain features, and a correlation is noted between the development of patterned wings and the acquisition of a tectiform wing-posture.

INTRODUCTION

In 1966, while exploring the British Museum (N.H.) collection of Baltic Amber fossils, I came across a fine male of a new species of the tabanid genus *Haematopota* (fig. 1); this genus was not previously known in the fossil state. According to Hennig (1967: 42-49), the only horsefly species recorded in the Baltic Amber fauna had been the chrysopsine *Silvius laticornis* Loew. It seemed a pity that the specimen should remain in obscurity, so I borrowed it in 1974 for study. I then discovered that a member of the psychodid genus *Phlebotomus* previously observed in the same block of amber also belongs to an undescribed species. That representatives of these two important groups of blood-sucking flies were entombed together is a strange coincidence. However, there are also two other insects: one is a small bee, apparently a meliponine, awkwardly situated at the edge of the block and difficult to study, and the second is a ponerine ant represented by its head and part of the thorax. Few pieces of amber could rival this one for the variety of its inclusions!

I am grateful to Mr B. H. Cogan for kindly searching out the specimen for me and retrieving a note left with one of T. D. A. Cockerell's fossil insect types, and Dr Morris for allowing me the loan of the specimen from the Department of Palaeontology. My research at the British Museum (N.H.) was supported by a Senior Bursary awarded by the South African Council for Scientific and Industrial Research.

Family PSYCHODIDAE

Subfamily Phlebotominae

Unfortunately the sandfly (see fig. 1) is positioned at an awkward angle to the viewer owing to the way in which the amber has been trimmed, and the wings in particular cannot be seen other than in oblique view. The thickness of the block makes an examination with a microscope objective more powerful than X20 impossible.

The history of the classification of phlebotomines into genus-group taxa is extraordinarily complex, mainly as the result of differing importance being accorded to

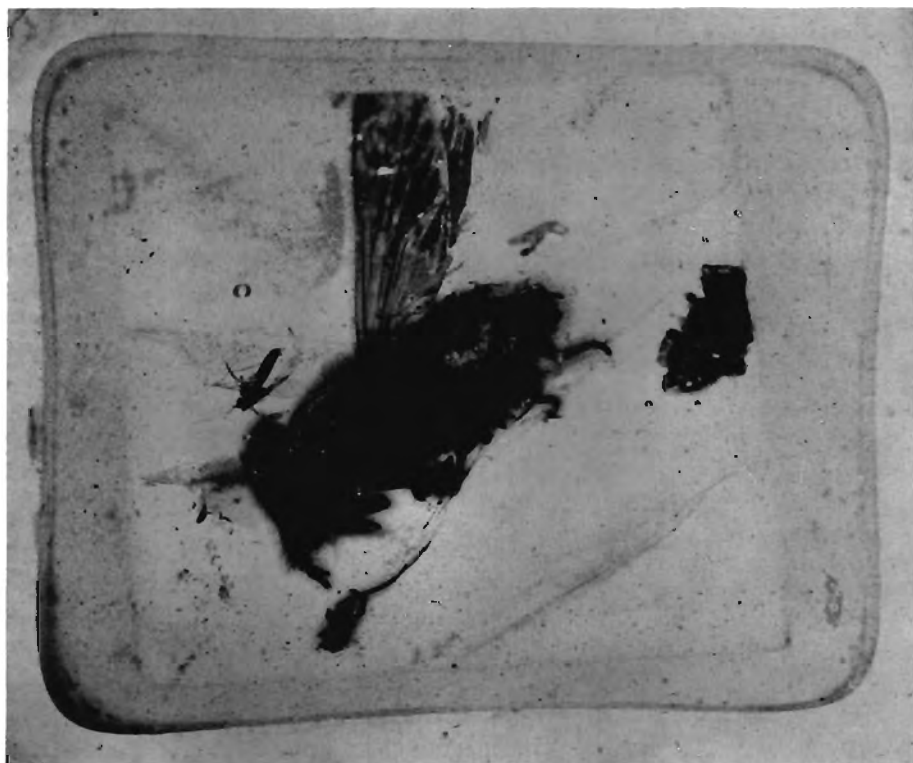


Fig. 1. The block of Baltic Amber with its four insect inclusions (see Introduction).

particular characters by various authors. Abonnenc (1972: 68) says, with justification, 'La classification des Phlebotomes au niveau des genres reste délicate . . .'; his classification of the subfamily (op. cit.: 73-76), one of the more recent available, is adopted here. In Abonnenc's key the specimen comes out with no difficulty as a member of the genus *Phlebotomus* Rondani *sensu* Abonnenc; indeed, it seems to be a fairly typical representative. The only notable features in which it is exceptional are the rather rounded form of the wing (fig. 5, but it should be noted that the other wing, which can be seen only obliquely to the longitudinal axis, appears to be more pointed apically), and the presence of only one ascoid per flagellar segment.

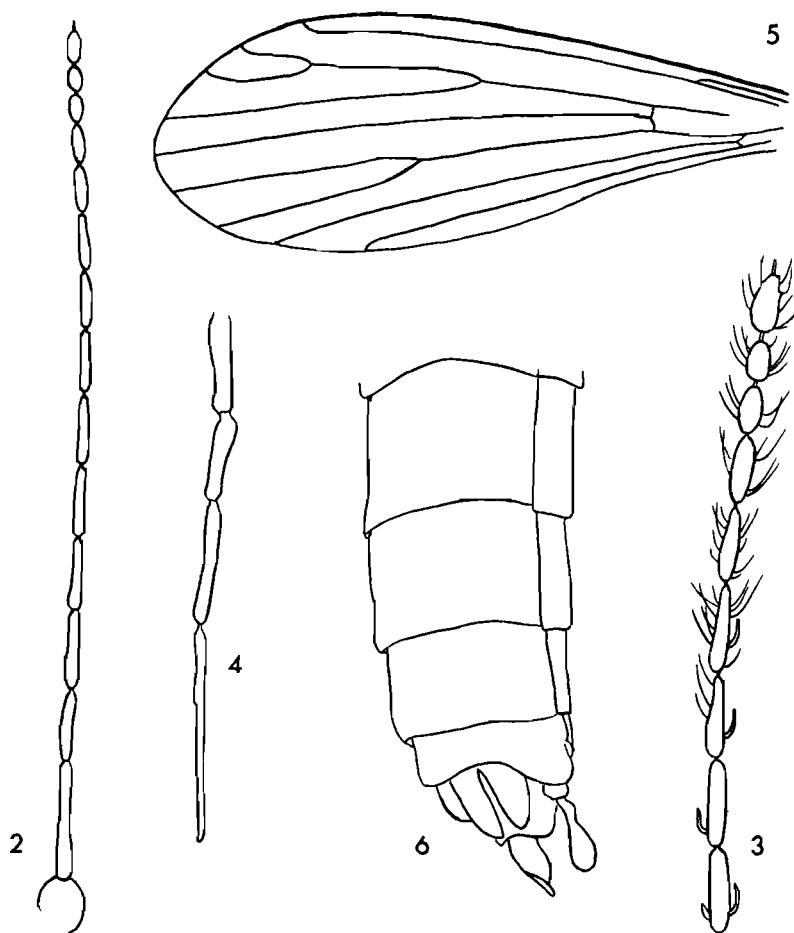
Genus *Phlebotomus* Rondani (*sensu* Abonnenc, 1972)

Phlebotomus succini sp. n.

Diagnosis: A rather small species, as preserved uniformly light brownish. Easily distinguished in the female from the only other known species in the Baltic Amber fauna, *P. tipuliformis* Meunier, by the relatively much shorter third antennal segment (fig. 2) (in *tipuliformis* segment 3 longer than $4 + 5$, ratio 38 : 21), moniliform apical antennal segments (uniformly subfiliform in *tipuliformis*), and relatively much longer fifth palp segment (in *tipuliformis* segment 5 only a little longer than 4, ratio 10 : 12); the wing veins of the two species differ considerably in proportions, mainly because in *tipuliformis* r-m and the origin of R_5 are nearer the centre of the wing (about $\frac{2}{5}$ of the

wing length away from the base), whereas in *succini* (fig. 5) they are much nearer the base. (Data on *tipuliformis* from Hennig 1972, figs 49, 51, 53.)

Description: ♀. Third antennal segment extending beyond tip of proboscis, shorter than $4 + 5$ (ratio 26 : 33), about 14% of total length of flagellum (3–16) (see fig. 2): right antenna denuded except for a few of the apical segments which have only setae; left antenna better preserved but curving away from viewer so difficult to examine—segments 3–11 each apparently with one sub-basal ascoid, but those on 3–5 not clearly visible, formula I/III–XI, the ascoids on 8–11 large (fig. 3); segments 3–11 filiform, 12–13 more stoutly filiform, 14–16 moniliform. Palp as in fig. 4, segments 2 and 3 subequal, each shorter than 4, segment 5 long and slender, ratio 21 : 20 : 28 : 48, formula 1–3–2–4–5; apex of segment 2 extending to tip of proboscis; Newstead's scales possibly present on segment 3. Abdominal tergites largely denuded, but some long hairs present both discally and on posterior margin, as preserved these hairs erect, but this possibly not natural; hair sockets not visible; apex of abdomen as in



Figs 2–6. *Phlebotomus succini* sp. n. (2, 3) entire antenna, and apical nine segments; (4) maxillary palp; (5) wing; (6) latero-ventral view of apical part of abdomen.

fig. 6. Wing (fig. 5) with R_{2+3} longer than R_2 and subequal to R_{2+3+4} ($\gamma/\beta = 1,0$ approx.); fork of R_2 and R_3 short; R_1 clearly curved forward at end, overlapping R_2 by only a very short distance. Fore femur subequal to length of tibia, ratio 20 : 19; middle femur subequal to tibia length, ratio 21 : 22.

Wing length 1,35 mm approx.; wing width 0,43 mm. Body length, excluding mouthparts, including cerci, 1,45 mm. Total antenna length 1,07 mm. Combined length of palp segments 2-5 = 0,57 mm.

Holotype ♀, in same block of Baltic Amber as holotype of *Haematopota pinicola* sp. n. See p. 461.

In Abonnenc's key to the eight subgenera of *Phlebotomus* which he recognizes, *succini* cannot be traced satisfactorily as the distribution of scales on the pleura is indeterminate because of a film of air covering much of the thorax, and of course the spermatheca cannot be seen. However, in only one of these subgenera, the African *Grassomyia* Theodor, does the female have a single ascoid per flagellar segment. In *Grassomyia* the ascoid formula is 1/4-15 (one ascoid on each of segments 4-15); the fossil appears to lack ascoids on the terminal five segments (fig. 3) so its formula could be 1/3-11, but the presence of ascoids on 3-5 is not certain. As the ascoids are specialized setae, it is possible that a single ascoid per segment is a more plesiomorphic condition than two or four; however, the species of *Grassomyia* show no other feature that might be considered primitive. All the species of *Grassomyia* have the third antennal segment shorter than $4 + 5$ ($3 < 4 + 5$) as in the fossil, but it is questionable whether *succini* is a member of that subgenus.

The only other phlebotomine known in Baltic Amber, *Phlebotomus tipuliformis* Meunier, differs conspicuously from *succini* in the relative proportions of the palp and antennal segments and certain of the wing veins (see the diagnosis given above). Hennig (1972: 51-55) discussed the relationship of *tipuliformis* at length, mainly with reference to the controversial classification of Old World Phlebotominae proposed by Theodor (1948). He concluded that the species possibly belongs in *Phlebotomus* Rondani *sensu* Theodor (a more restricted concept than Abonnenc's), and as it appears to have a trilobed genital style, may be related to or belong in one of the subgenera *Phlebotomus* s. str., *Anaphlebotomus* or *Euphlebotomus*, which were erected or defined by Theodor but not recognized by later workers. Hennig understandably declined to allocate *tipuliformis* to any of these groups.

The original description of *tipuliformis* by Meunier (1905: 254, pl. VI, figs 14-18) and the account of it by Hennig (1972: figs 49-56) reveal the species to be unusual in some features whose significance was not discussed by either author. The most noticeable of these is the proportionate length of the palp segments. From Hennig's drawings it appears that the apical four segments of the male are proportioned 5,5 : 7 : 6 : 9 (formula 1-2-4-3-5), and the female has the last three segments proportioned 15,5 : 10 : 12. The shortness of the fifth segment in both sexes is unusual; the condition in the female, which has the third segment the longest, is highly exceptional. According to Abonnenc (1972: 41) the fifth segment is always the longest in the entire fauna of Ethiopian Region phlebotomines; the segment is much reduced or primitively short only in certain neotropical taxa (*Brumptomyia* França & Parrot, *Lutzomyia* França—see Lewis 1973: 162). Furthermore, the wing of *tipuliformis* (Hennig op. cit.: fig. 53) has a rounded end not typical of modern *Phlebotomus* species, and the propor-

tions of certain of the veins are also not typical, mainly because r-m and the origin of R_5 are nearer to the centre of the wing. Vein R_{2+3+4} is thus unusually short, and if the ratio γ /wing breadth (see Abonnenc 1972: 74; Kirk & Lewis 1951: 400, or other accounts of Phlebotometry) is measured from Hennig's drawing, the value 3,6 is obtained. According to Abonnenc (op. cit.: key, p. 75) this ratio is always less than 3,5 in *Phlebotomus*; in *succini* the ratio is 1,4.

Hennig's account of *tipuliformis* is subsidiary to his description of a new phlebotomine genus, *Phlebotomites* Hennig, based on two new species occurring in lower Cretaceous amber from Lebanon. He distinguishes this genus from *Phlebotomus* in the broad sense by its rather wide, apically rounded wing. However, if the wing of *Phlebotomites brevifilis* Hennig (his fig. 23) is compared with that of *tipuliformis* (his fig. 53), a close similarity in shape is evident. The wings are also alike in that the distance γ is short because of the more distal position of r-m and the origin of R_5 . But the most striking similarity is in the proportions of the palp segments; unfortunately these can be compared only between *tipuliformis* and *Phlebotomites brevifilis* as the unique specimen of *Phlebotomites longifilis* lacks the palps. The male of *brevifilis* as shown in Hennig's fig. 14 has the palp segments proportioned 5,5 : 11,5 : 7,0 : 9,0; thus the apical segment is relatively short, and the longest segment is the third, in this uncommon feature resembling the female of *tipuliformis*.

On the evidence published it seems that *tipuliformis* is in some respects intermediate between *Phlebotomus sensu* Abonnenc and *Phlebotomites*. Indeed, the two species of *Phlebotomites* could be considered congeneric with *tipuliformis* in which case *Phlebotomites* becomes a synonym of *Phlebotomiella* Meunier (1906: 103), a genus erected for *tipuliformis* subsequent to the description of that species but not discussed by Hennig and largely ignored by other workers. In *tipuliformis* the male genital style has four spines, whereas both species of *Phlebotomites* have five, but this sort of difference is considered by present-day Phlebotomists to be important usually at the species level only. If this relationship is correct, the two species in Baltic Amber are significant for different reasons: *tipuliformis* suggests the persistence with little change of a relatively primitive phlebotomine stock in the western Palaearctic over a vast period of time (from early Cretaceous to early Tertiary), whereas *succini* is evidence that a virtually modern *Phlebotomus* type was, broadly speaking, coeval and sympatric in the Eocene.

Family TABANIDAE

Subfamily Tabaninae

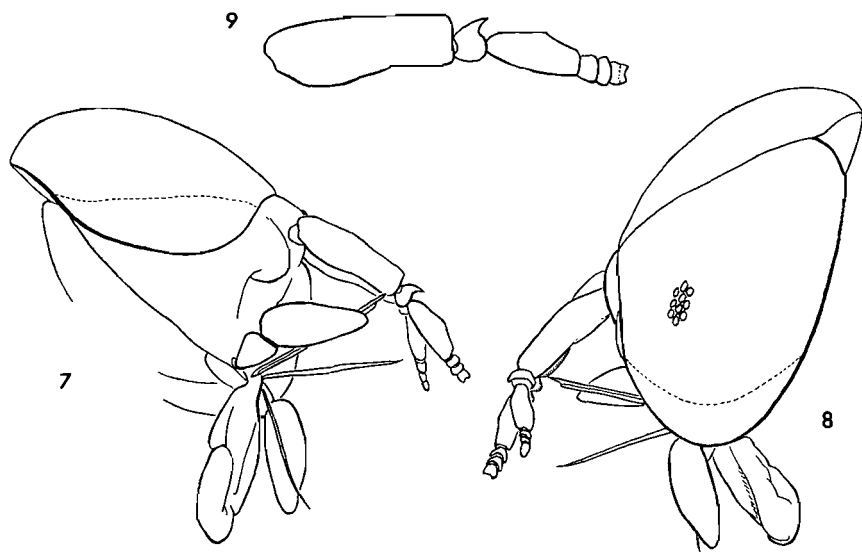
The identity of the specimen described below as a member of the genus *Haematopota* Meigen is apparent at a glance and is confirmed by a detailed examination. Because the apex of the abdomen is missing, important taxonomic characters in the genitalia are not available. However, membership of the subfamily Tabaninae is established by the lack of ocelli and hind tibial spurs; in addition, vein Sc is setulose below and R_4 has a strong appendix (Mackerras 1954: 439). The fly is indubitably a member of the tribe Haematopotini as defined by Mackerras (loc. cit.): there are only three annuli after the third antennal segment, the first segment is elongate, the third segment has only a slight dorsal angle, the palpi are swollen, and the wings are characteristically patterned. The basicosta cannot be seen clearly, so the presence of setulae cannot be

established. Within this tribe (as discussed by Moucha 1969) the fossil clearly falls in the genus *Haematopota* as it has the typical wing pattern of pale rosettes on a dark ground that distinguishes the genus from the African *Hippocentrum* Austen, the Palaearctic *Heptatoma* Meigen, and the Oriental *Hippocentroides* Philip. In fact, the fossil would not be considered remarkable among the living members of the genus, except perhaps on account of its antennae. It is a typical male *Haematopota*, with broad head, enormous eyes each subdivided into a major upper part with large facets and a minor lower part with tiny facets, somewhat flattened body, much swollen palpi, and relatively short legs. It has a feature used in the taxonomy of the living species, namely the presence of pale tibial rings, and resembles them also in having conspicuously pale middle and hind basitarsi.

***Haematopota pinicola* sp. n.**

Diagnosis: A fairly small species with bare eyes in the male; first antennal segment irregularly subcylindrical, diameter of its apical portion about 28% of its length; second antennal segment with a strong dorsal point; third antennal segment only half as long as first segment, its upper margin with an obtuse angle at about midlength; flagellar segments deeper than long, apical one slightly concave on anterior margin; pale tibial rings 0.2.0; basitarsi of middle and hind legs largely pale; wing rosette pattern simple. The form of the antenna of *pinicola* cannot be matched in the figures given by Olsufjev (1937), Leclercq (1967), and Chvála, Lyneborg & Moucha (1972) for modern Palaearctic species.

Description: ♂. Head of normal form (figs 7, 8); eyes bare, lower area of small facets sharply defined, restricted as indicated on figures. Antenna as in fig. 9; first segment elongate subcylindrical, of irregular form, not rounded in cross-section especially over basal half where there is a ventral bulge and a ventro-lateral, sublongitudinal



Figs 7-9. *Haematopota pinicola* sp. n. (7, 8) Head in latero-ventral and latero-dorsal views; (9) right antenna, outer aspect.

impression on outer side; there is no evidence that any part of first antennal segment was polished. Second segment with prominent dorsal point. Third segment relatively short, only half as long as first, with definite, obtuse angle at about midlength on dorsal surface. Three flagellar segments as figured, all deeper than long, apical one shallowly concave on anterior edge and with an indefinite subdivision at midlength. Palps as in figs 7 and 8, swollen, rounded in cross-section. Labrum and maxillary stylets exposed.

First antennal segment, parafacials and palpi with long, brown hairs; second segment shorter-haired above and below; third segment dorsally with some short hairs basad of angle and slightly longer hairs irregularly along ventral surface. Hairs of postoccipital fringe long, brown. Mesonotum and scutellum with long, erect, pale brownish hairs. Tergites of basal part of abdomen with similar hairs.

As preserved, colour of thorax and abdomen reddish-brown; antennae uniformly brownish; mouthparts pale yellowish-brown; forelegs brownish except darkened tarsus and paler base of tibia; middle legs with sub-basal and pre-apical pale tibial bands and pale basitarsi, otherwise more or less unicolorous brownish; hind legs uniformly brown on femur and tibia, but with a contrastingly pale basitarsus except for its darkened apex. Spurs on mid-tibia unequal, posterior spur about half length of anterior one.

Wing venation normal, R_4 with strong appendix. Observable elements of wing pattern shown in fig. 10; pattern in posterior cells indistinct or obscured by overlying air films.

Mesonotum length 2,0 mm; head width 3,3 mm; head height excluding mouthparts, 1,7 mm; wing as preserved 6,2 mm long, thus complete wing length probably about 7,0 mm; wing width across stigma 2,2 mm.

Holotype ♂, in Baltic Amber; the block has been trimmed and mounted in balsam, and the slide bears an old label reading 'Gum Copal Inclusa. Stettin on Baltic. 58588.' The left wing and apex of the right wing are missing, and the apical half of the abdomen has been lost across an oblique break. In the British Museum (N.H.), London.

The wing pattern of Haematopota

That this fossil of Eocene age should be so extremely similar to the Recent species of *Haematopota* is certainly interesting, but somewhat disappointing as the specimen throws no light on the origin of the genus or evolution of its special features. The

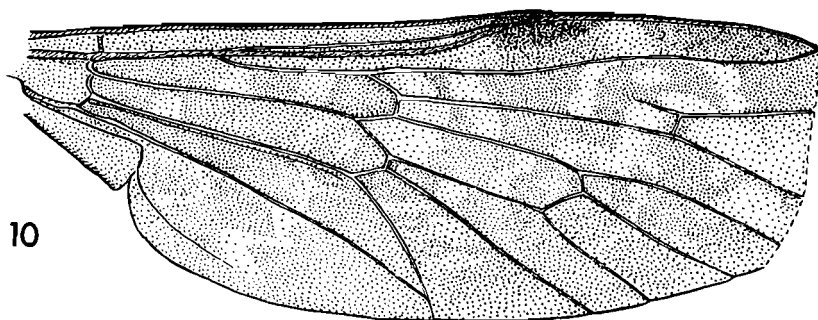


Fig. 10. *Haematopota pinicola* sp. n. wing.

presence in the fossil of the highly characteristic wing pattern is of particular note. Oldroyd (1952: 15–17) has discussed this pattern with regard to the Subsaharan species and describes how it is made up of two elements: a staining of the membrane and a vestiture of microtrichia. He states that the pattern is produced mainly by the colour of the microtrichia, and that all the microtrichia of the lower wing surface are dark, whereas on the upper surface they are dark except in the rosettes where they are pale. My studies, however, indicate that this is true only for certain species of *Haematopota*.

The distinctive African *denshamii*-group contains a number of species distributed in tropical savannas around the equatorial forest biome (Oldroyd 1952: 27); all are tawny or greyish, with an unusually pale wing due mainly to the spreading and coalescence of rosettes. The wing of a typical member of the group, *H. brunnipennis* Ricardo (see Oldroyd op. cit.: fig. 186), has the dark component of the pattern created to a considerable extent by stained patches of variable intensity in the membrane. In these stained patches, and also in quite extensive unstained areas, the microtrichia are dark on both sides of the wing; in the rosettes the membrane is uncoloured and the microtrichia are small, weak and pale on both sides.

The highly unusual, blackish, silvicolous species *H. nobilis* (Grünberg) is unique in *Haematopota* as it has a uniformly very dark wing apart from a narrow, pre-apical, pale fascia. In transmitted light the membrane appears extensively brown-stained, but the centres of many cells are paler, and the base of the marginal cell, the two basal cells and axillary cell are greyish. The microtrichia are evenly distributed, darkly coloured and equally sized on both wing surfaces, except in the pre-apical fascia where the membrane is whitish and the microtrichia are smaller, paler and finer on both sides of the wing. The wing of *Hippocentrum stringipenne* Karsch is patterned in the same way.

In *H. obscura* Loew, a member of the *tumidicornis*-group, which is a blackish, silvicolous species with a richly patterned wing, the membrane in transmitted light is yellowish-brown, even in the rosette areas, and there are conspicuous greyish patches in many of the cells. The microtrichia are dark above and below everywhere except in the rosettes where they are finer, a little more sparse and paler on the upper side, and slightly sparser but otherwise undifferentiated on the lower side. The covering of the microtrichia darkens the wing in the area outside the rosettes.

It appears that staining of the membrane is the dominant factor in the pattern, for it determines the colour and density of the dark component; the formation of rosettes is due to the absence of staining combined with the reduction in size and loss of colour of microtrichia on one or both surfaces.

The specimen in Baltic Amber appears to have a pale, weak pattern, but this may be due to its age or the medium in which it has been preserved. Its pattern is produced largely by staining, and there are both brown- and grey-stained patches. In the stained areas the microtrichia are dark above and below, but in the rosettes they are finer and pale on both sides of the wing. Thus the wing of *pinicola* is similar to that of the living savanna species *brunnipennis* in the way the rosettes are formed, but unlike that species in the nature of the rosette pattern. A far more extensive study of *Haematopota* wings would be necessary before one could conclude with confidence that the wing of the fossil indicates a non-forested, warm savanna habitat. However, the implication is

supported by the bare eyes of the male *pinicola*; all living European *Haematopota* species of which both sexes have been described have hairy-eyed males, a condition usually associated in Tabanidae with life in cool, humid climates. A possibility that Baltic Amber fauna lived in a Mediterranean-type climate, with warm, dry summers, has been suggested by Ross (1966: 280).

Oldroyd (op. cit.: 16, fig. 8) also discussed the fundamental features of the *Haematopota* wing pattern. Many of these features are present in the fossil (fig. 10); there is the strong rosette around the base of R_4 and its appendix, a clear area in the marginal cell apicad of the stigma, a zigzag mark and pale basal streak in the axillary cell, and a system of rosettes centred on r-m and the base of the fourth posterior cell. Oldroyd reached no definite conclusion about which type of pattern is primitive in *Haematopota*, though he decided that an almost uniformly dark wing with few pale markings probably is not primitive. On this subject the fossil provides little information; it has a rather simplified version of the basic pattern for the genus as a whole.

Any consideration of the evolution of the distinctive *Haematopota* wing pattern should take into account the fact that the presence of the pattern is correlated with a resting wing posture that is particularly characteristic of the Haematopotini. Three of the four included genera—*Haematopota*, *Hippocentrum* and *Heptatoma*—hold the wings in a roof-like or tent-like pose; no information is available on the wing posture of species in the rare Oriental genus *Hippocentrodes*. Only one of these genera, the monotypic, temperate Palearctic *Heptatoma*, has clear, unpatterned wings, and it should be noted that its inclusion in the tribe is in some doubt in view of its larval features (see illustrations by Ježek 1971) and lack of subcostal setulae (Mackerras 1954: 439). The evolution of a disruptive, complex pattern in conjunction with such a wing posture is possibly advantageous in providing camouflage for the flies when at rest. If the pattern evolved to provide crypsis after attainment of the tectiform posture, it is likely that the primitive pattern would be one that included disruptive components from the outset. There is a comparable case in the acalyptrate family Lauxaniidae; the members of a few genera (e.g. *Cestrotus*, *Cainohomoneura*) in the Homoneurinae are exceptional in holding the wings in a tectiform posture while at rest or walking, and all have boldly patterned wings that camouflage the flies against their preferred substrates of stone or bark. Curiously, many of these lauxaniids have the eyes multicoloured and adorned with irregular horizontal bands, to quite a considerable extent resembling the spectacular eyes of living *Haematopota*.

The age of the genera of Tabanidae

Mackerras (1954: 440, 452) considers that the Tabanidae diverged early in the Mesozoic, their sister-group being the Athericidae (Stuckenberg 1973), with the result that the subfamilies, tribes and some genera were established by the middle Mesozoic, and after a period of quiescence there was a vigorous Tertiary evolution of more specialized tribes and genera. Fairchild (1969: 8) concurs, and considers that the subfamilies certainly, and the tribes probably, were established before the Tertiary, possibly in the early Cretaceous. The occurrence of a typical member of the genus *Haematopota* in the Eocene Baltic Amber supports their hypothesis.

Moucha (1972) reviewed the known fossil tabanids and listed seven species and one infraspecific taxon. One of the species, *Chrysops vectensis* Cockerell (1921), described

from a well-preserved wing from the Oligocene of the Isle of Wight, is generically misplaced. Mr Oldroyd and I examined the type in December 1965 and found that the ventral side of the wing was preserved and has subcostal setulae; we concluded that there is no evidence that the species is a *Chrysops*, but that it more probably belongs in *Tabanus*. With this amendment, the fossil record is as follows: *Chrysops* is known from the Eocene of France; *Silvius* from the Miocene of North America; *Tabanus* from the Oligocene of France, the Pliocene of Germany, and probably the Oligocene of the Isle of Wight; and *Haematopota* from the upper Eocene Baltic Amber. The Baltic Amber species *Silvius laticornis* Loew appears to be a chrysopsine but is wrongly placed generically (Hennig 1967: 47) and requires further study.

Mackerras (op. cit.: 450) considers the Haematopotini are probably of comparatively recent origin and derived from a *Dasybasis*-like ancestor, but it appears from the evidence of *pinicola* that the tribe must be older than he suggests. Radiation of some tabanid genera may have occurred during the Tertiary, but most of the genera must have been differentiated before the end of the Mesozoic. Haematopotini probably arose in wooded parts of the Old World tropics when the ancestral form acquired the wing-flexing mechanism necessary for the tectiform posture.

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